Avicennia germinans (L)L. Black Mangrove

Avicenniaceae Verbena family

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HABITAT

Native Range

Avicennia germinans (L) L., the black mangrove, occurs in most of the mangrove forests of the American coastal areas (fig. 1). It is found throughout the coast of the Gulf of Mexico, and from northern Florida (29°53′ N) to Espiritu Santo, Brazil (approximately 23° S). On the Pacific coasts of North and South America, it grows from Punta de Lobos, Mexico (30°15′ N), to south of Punta Malpelo, Peru (3°40′S) (*11, 64*).

Black mangrove grows in tidal areas with salty or brackish waters. It grows well in basin forests over a broad range of soil salinities (*23, 30*). The best structural development is attained in tropical wet riverine forests (*23*). Black mangrove also grows in the less flushed inner portions of fringe and riverine forests. In these areas it shows a distinct preference for slightly higher drier soils (*55*). At the geographical limit of mangrove distribution, black mangroves occupy the forest fringe (*33*).

Climate

Black mangroves grow over a wide variety of climates. They grow in tropical and subtropical dry, moist, and wet life zones, with a broad range of precipitation regimes (from 800 to 7,000 mm per year).

The species is sensitive to frost, but of all the mangrove species, it is considered the most tolerant to low temperatures (*12*). In its northern limits of distribution, black mangroves are killed by freezing temperatures –3 to –11°C) (*33, 64*). In these areas, tree heights are shorter relative to trees growing at lower latitudes. Black mangrove is the dominant species on sites with arid climates, where soil salinities exceed 40 parts per thousand (*13*).

Soils and Topography

Black mangrove distribution is highly influenced by changes in microtopography and the consequent changes in soil flooding and salinity (*10, 14*).

The species is usually found in low areas, inland from the fringe of the mangrove forest. However, it also grows inland, on slightly elevated areas, where tidal flooding is less frequent. Here soils are covered by a few centimeters of continuously standing water or are inundated only a few times per year (213 to 432 tides per year, *10;* 152 to 158 tides per year, *58*).

Black mangrove grows on sandy, silty, or clay soils. It is found on heavily oxidized clays or on soils with significant concentrations of pyrite (*2*). Black mangrove soils have organic matter contents of 2 to 25 percent (*23*), but values may be as high as 58 percent (*34, 58*); nitrogen content is low—around 0.4 percent (*20*).

The species can grow on soils where salinities range from 0 to 100 parts per thousand (*51*). Under high soil salinities, structural development is suppressed (*13*). Leaves excrete salt through specialized glands and may be salt covered, thus contributing to salty throughfall (*31*).

Associated Forest Cover

Black mangrove may be found in pure stands or in close association with other mangrove species within its range. It grows with *Rhizophora mangle* L., *R. harrisonii* Leechm., *R. racemosa* G.F.W. Meyer, *Avicennia*

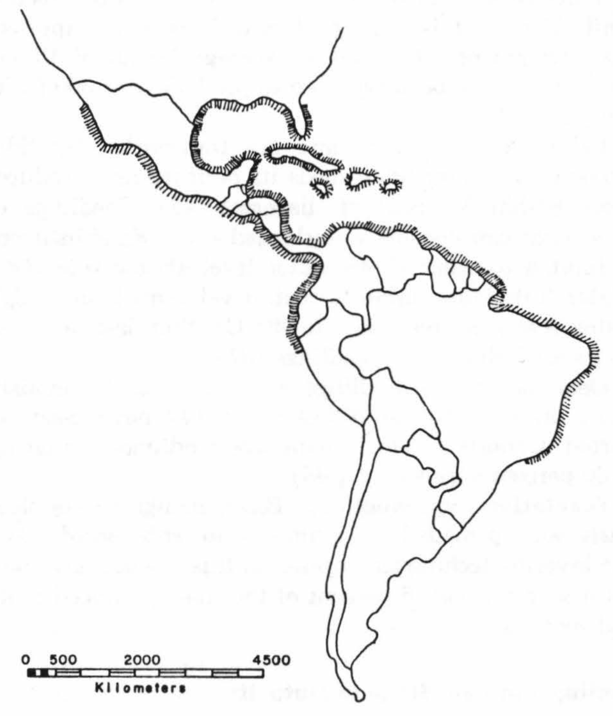

Figure 1.—*Distribution of* Avicennia germinans *in the New World.*

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tonduzzii Moldenke, *A. schaueriana* Stapf & Leechm., *A. bicolor* Standl., *Laguncularia racemosa* Gaertn., and *Pelliciera rhizophorae* Tr. & Pl.

In basin forests, where soil salinities are around 30 to 40 parts per thousand, black mangrove grows with white mangrove (*L. racemosa*); if soil salinities are higher than 50 parts per thousand, the black mangrove will be dominant (*14*). In areas of low soil salinity, black mangrove may be associated with *Pterocarpus officinalis* Jacq., *Mora oleifera* (Triana) Duke, *Conocarpus erecta* L., and the fern *Acrostichum aureum* Troll, Sloane, Hooker.

LIFE HISTORY

Reproduction and Early Growth

Flowering and Fruiting.—Flowers are found in axillary and terminal inflorescences, with 1 to 15 pairs of flowers per spike. They are small (1 to 2 cm wide), sessile, and with imbricate bracts. The corolla has four lobes. Petals are yellow or cream to white, generally with a yellowish throat (*10, 38*). The fragrant insect-pollinated flower has a two-celled ovary; each loculus contains two locules (*39*). Flowering is sporadic throughout the year, even though distinct peaks can be observed (*36, 45*). Sexual maturity is reached when plants are 2 to 3 m tall (*26*).

The species is considered viviparous because germination occurs while the embryo is still enclosed in the fruit. A distinctive seedling develops before the fruit falls from the parent tree. The expansion of the cotyledons and the development of plumular leaves is evident (*54*).

Three of the four ovules abort, producing a one-seeded fruit. The fruit is oblong or elliptic with an approximate weight of 1.1 g and an average length of 1.8 cm (*6*). Trees have been reported to produce over 300 fruits per year (*10*).

Fallen seedlings float and are transported by tidal currents. The propagule sheds its pericarp and produces roots within 3 weeks of dispersal (*45*). Seedlings of *Avicennia* can become waterlogged (*15*). Establishment is limited to areas above water level at low tide (*64*). Water turbulance inhibits root development, and high water temperatures (39° to 40°C) that last over 48 hours are lethal to the seedlings (*37*).

Densities of 0.07 seedlings/m^2 (*34, 58*) and establishment rates of 0.06 seedlings/m^2•yr (*4*) have been reported. Cohorts of black mangrove seedlings exhibit up to 30 percent survival (*17, 46*).

Vegetative Reproduction.—Black mangrove coppices fairly well, provided the stump is not submerged (*36*). Air layering techniques applied to this species have had little success; only 6 percent of the trees produced roots and rootlets (*6*).

Sapling and Pole Stage to Maturity

Growth and Yield.—Black mangrove growth is characterized by continuous growth of the axes (i.e. Attims's model, *19*). Branching is diffuse with slightly slanting secondary axes (*26*). Growth rings are produced, and the number of rings and the average diameter of the section appear to be related. However, the number of rings are not related to age (*18*). Diameter-age measurements for black mangrove individuals in the Caribbean show average diameter at breast height (d.b.h.) of 8.6, 12.2, and 19.1 cm for trees 10, 20, and 50 years old, respectively (*43*).

Planting of wildlings (0.6 m tall) has given poor results (*21*). *Avicennia* spp. in the Indo-Pacific region are planted by planting seedlings during periods of low tide (*56*).

Plants 0.5 to 1.5 m tall, transplanted with a rootball 1.5 times wider than tree height, had good recovery (*44*). Pruned saplings grew 3.9 times faster than unpruned controls (*44*). Tree stature varies enormously, with some mature (reproductively active) individuals only 20 cm tall and others growing to a height of 36 m with a d.b.h. of 1.8 m (fig. 2). Climatic and edaphic conditions are responsible for this variability (*13, 23*). In the Caribbean, black mangrove forests generally do not exceed 15 m, even though on the wet Central American coast, individual trees more than 30 m in height can be found. Monospecific black mangrove basin forests in south Florida have basal areas of 12.5 to 21.2 m^2/ha, and tree density ranges from 2,467 to 6,511 trees/ha (*34, 58*).

In riverine forests in Venezuela, parcels dominated by black mangroves had wood volumes of up to 350 m^3/ha (*35*). In Puerto Rico, periodic annual diameter increment was 0.42, 0.46, and 0.51 cm per year in three replicate stands over a 37-year period after clearcutting (*62*). Periodic basal area growth (table 1) decreased with age. These results are for black mangrove growing in stands dominated by white mangrove (*L. racemosa*).

In Venezuelan riverine forests, 20-by 300-m parcels rotated every 30 years are used as management units (*35*). *Avicennia* spp. in India have been used with a clear-felling system and 15 to 25 year rotations. Here, 50 to 60 trees/ha are left as seed trees (*12*).

Net primary production rates ranging from 0.94 to 2.7 gC/m^2•day have been measured in black mangrove forests growing in water with a low chlorine content (5 to 16 parts per thousand) (*7*). Gross primary productivity (averaging 8.62 gC/m^2•day) (*31*) increases with increasing chlorinity between the range of 5 to 16 parts per thousand (*7*). Wood production in a disturbed forest was 1.74 g/m^2•day (*31*). The complexity index (*22*) of black mangrove stands in south Florida decreased from 40 to 3.4 when soil salinities increased from 40 to 65 parts per thousand (*34, 58*). Water loss via transpiration from black mangroves was 2.53 mm per day relative to 4.19 mm per day for adjacent red mangroves (*31*).

Rooting Habit.—Black mangrove is characterized by a shallow underground root system with thin sinker roots and negatively geotropic pneumatophores that develop from lateral horizontal roots (*24*). Soft, slender roots occassionally emerge from the trunk of old trees (*39, 50*). Pneumatophores are responsible for gas ex-

Figure 2.—*A mature* Avicennia germinans *tree.*

Table 1.—*Basal area growth in three Puerto Rican mangrove stands clearcut in 1937.* Avicennia *comprised between 2 to 6 percent of the stems in 1938 and between 20 to 30 percent in 1975.*[1]

Time interval	*Laguncularia racemosa*	*Avicennia germinans*	Total
years		*m²/ha. yr*	
1938–1945	...	...	0.18
	...	...	1.20
	...	...	1.48
1945–1949	2.8	0.44	3.24
	2.17	0.37	2.54
	0.92	0.29	1.21
1951–1955	0.77	0.58	1.35
	0.71	0.31	1.02
	0.63	0.48	1.11
1955–1975	0.67	0.08	0.75
	0.94	0.12	1.06
	0.71	–0.04	0.67

[1] Data adapted from Weaver 1979 *(62).*

change processes (*32, 49*). An average density of 672 pneumatophores/m² has been measured in basin forests of south Florida (*4, 58*). However, the actual number of pneumatophores is highly variable (*2*). Pneumatophore height increases with increasing water depth (*29*).

Root biomass in *Avicennia* species may account for up to 65 percent of the total tree biomass (*16*). Fibrous roots comprise approximately 50 percent, while pneumatophores and lateral roots each comprise approximately 25 percent of the total root biomass (*16*). Fast root production rates allow the species to become established on rapidly accreting shorelines and adjust quickly to rapid sedimentation (*64*).

Reaction to Competition.—Black mangrove is considered intolerant of shade and is unable to regenerate in even moderate shade (*61, 45*). In areas where there is constant flushing, black mangrove is dominated by other mangrove species. In the inner parts of the forest under low soil salinity conditions, brackish water species such as *Pterocarpus officinalis* and *Mora oleifera* outcompete black mangrove (*12*).

Damaging Agents.—The wood borer *Sphaeroma terebrans* Bate has been found in exposed roots of black mangrove trees (*48*). The fungi *Alternaria alternata* and *Phytophtora* spp. have been reported as the cause of defoliation and death in Australian *Avicennia* spp. (*9, 41*). Leaf infestation and defoliation by the scale *Icerya seychellarum* Westw. and the caterpillar *Cleora injectaria* Walker have been observed in *Avicennia* spp. of the Indo-Pacific (*40, 42*). It is common to see a high intensity of leaf miner activity in black mangrove trees.

Black mangrove is highly susceptible to changes in hydrological patterns. Drought or flooding can cause extensive mortality (*3*). The species is easily wind thrown and is killed when exposed to low concentrations of auxin-type herbicides (*57, 60*). The wood is susceptible to attack by dry-wood termites (*28*). Others report the wood to be termite resistant but heavily damaged by fungus and marine borers (*1, 52*).

SPECIAL USES

Black mangrove is used as a source of firewood and charcoal in many coastal areas of tropical America. It is also used for cheap beams, door frames, boat construction, piers, wharf posts, telegraph and power poles, and crossties (*12, 28, 59*). The wood responds adequately to impregnation treatment with creosote (*1*) and with copperized chromated borate and copperized chromated arsenate preservatives (*25*).

The wood has a specific gravity of 0.8 to 1.0 and a radial and tangential shrinkage of 7.1 and 10.2 percent respectively. Its hardness and modulus of rupture are classified as moderate (*1, 53*). Black mangrove wood is coarse and of uneven grain. The heartwood contains a lapachol compound that gives it a yellowish coloration (*36*). Its wood parenchyma is sparingly paratracheal and wood fibers are usually thick walled (*47*).

Black mangrove wood has been reported as suitable for fiberboard and paper pulp (*53*). It can be pulped successfully by the soda process; however, it must be mixed with other types of wood because of its short

fiber (*47*). Alpha cellulose contents are generally about 69 percent. The wood responds adequately to air drying.

Black mangrove wood has been reported as difficult to work (*47*), but others (*1*) have described it as adequate for saw milling. Little abrasion was observed in steel saws used to cut black mangrove wood at 22 m/s and a 40° cutting angle (*1*).

The bark of black mangrove is used as a source of tannins even though soluble tannin contents are only 5.5 to 12.7 percent, on a dry weight basis. Infusions from the bark are used as an astringent. The resin is used for treatment of ulcers, hemorrhoids, diarrhea, and tumors (*12*). Species of *Avicennia* are favored by beekeepers because they contribute to yields of good quality honey (*8*). Sprouting seeds are edible when cooked but poisonous raw (*28*). Salt for cooking or eating purposes can be obtained from salt-coated foliage (*28*).

Soil under *Avicennia* forests have been reported as suitable for land reclamation in Africa. The lower sulphides and organic matter contents of these soils prevent the drastic reduction of pH observed after drainage of soils in other mangrove forests (*20*).

Black mangrove is considered a soil stabilizer. In areas near the mean high tide level, black mangrove is believed to reduce current velocities and promote sedimentation (*5, 63*). Along rapidly prograding coasts, black mangroves are responsible for holding the deposited material (*2, 63*).

Black mangrove can also be a fast leaf litter producer. Litter–fall rates in monospecific mangrove forests show marked seasonality with peak production during the rainy season. Maximum rates fluctuate from 2.5 to 3.3 $g/m^2 \cdot day$, while minimum rates vary from 0.4 to 0.5 $g/m^2 \cdot day$ (*34, 58*). Annual rates of litter fall in monospecific black mangrove forests of south Florida average 4.5 to 4.7 t/ha (*34, 58*). The decomposition of this material results in a highly nutritious detritus that supports secondary production in adjacent estuarine waters (*58*). Black mangrove leaves leach organic matter readily and have low carbon to nitrogen ratios resulting in fast decomposition rates (*34, 58*). These conditions enhance the development of a complex food web that includes many commercially important species of fish, mollusks, and crustaceans (*58*).

GENETICS

Population Differences

The genus *Avicennia* has been reviewed by Moldenke (*38, 39*). This author separated the genus from the Verbenaceae, creating a new family, Avicenniaceae. Four species of *Avicennia* have been reported in tropical America: *A. germinans* (L) L., *A. bicolor* Standl., *A. tonduzzii* Moldenke, and *A. schaueriana* Stapf & Leecm.. Little (*27*) maintains *A. nitida* in place of *A. germinans* (L) Stearn. Many authors consider *A. africana* P. Beauv., a dominant species along the coast of West Africa, as being the same species as *A. germinans* (L) L.

The species is highly polymorphic, and large variation exists among populations growing under different conditions. Leaf size is one of the most variable parameters; some of this variation is due to soil salinity.

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